

RESPONSE

'Exciting statistics': the rapid development and promising future of hierarchical models for population ecology

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doi:10.1111/j.1469-1795.2012.00540.x

Many biologists might indeed find statistics dull or even terrifying (van Emden, 2008), but ecologists and wildlife biologists should be downright ecstatic with recent developments in statistical modeling. One of the most exciting advances in recent decades is the development of hierarchical models. Hierarchical or multi-level models are becoming increasingly common in population analysis, and with good reason. Indeed, Kéry & Schaub (2011) devote much of their final chapter to the 'Power and Beauty of Hierarchical Models', and among the many virtues they list for hierarchical models are simpler fitting of complex models, clarity of thinking about these models and a 'step-up' approach to model building (Kéry & Schaub, 2011). Simpler and clearer model construction is an important advantage of hierarchical models, and although this may be reason enough to choose a hierarchical approach to modeling ecological data, the benefits do not stop with the fitting of the model to data.

The property of shrinkage is a particularly important advantage of hierarchical models in ecology (Gelman *et al.*, 2004; Gelman & Hill, 2006; Ntzoufras, 2011; Cam, 2012; Schaub & Kéry, 2012). Shrinkage (or 'borrowing strength') refers to the assumption of random effects to be realizations of a process governed by a statistical distribution (Gelman *et al.*, 2004; Cam, 2012; Schaub & Kéry, 2012). This stochastic assumption means that realizations of the process (such as daily risk of mortality at sites, in the present case) that are poorly estimated because of small sample size, short study duration, etc., but that fall far from the population mean will be pulled toward the mean; those realizations that are strongly supported by data contribute more information about the distribution from which the stochastic realizations are drawn, and are pulled less strongly toward the mean (Gelman *et al.*, 2004; Gelman & Hill, 2006). Including random effects in models therefore allows the estimation of parameters for realizations with small sample sizes, guards against spurious conclusions, and increases the precision of parameter estimates for all realizations of the process of

interest (Gelman & Hill, 2006; Cam, 2012; Schaub & Kéry, 2012).

Another important benefit of hierarchical models is reduction in bias. Where unmeasured (or unmeasurable) variables affect a parameter of interest, estimates of that parameter can be biased; applying a random effect allows for such unobserved heterogeneity and reduces the bias associated with unmeasured covariates (Gelman & Hill, 2006; Cam, 2012). The many advantages of hierarchical models for animal conservation apply not only to shared frailty models (Heisey *et al.*, 2010; Griffin *et al.*, 2011; Halstead *et al.*, 2012), but also to modeling individual frailties in survival and reproduction (Cam *et al.*, 2002; Wintrebert *et al.*, 2005), accounting for heterogeneity in individual capture probabilities (Dorazio & Royle, 2003), discerning patterns among demographic parameters (Link & Barker, 2005) and combining inference for mark-recapture models (Rivot & Prévost, 2002; Calvert *et al.*, 2009; Papadatou *et al.*, 2010, 2012) among many, many other applications.

Although all commentators correctly acknowledge that algebraically identical hierarchical models can be analyzed under a frequentist or Bayesian approach, the latter offers the ecologist several important advantages. Modern software allows the simple implementation of complex models that would be difficult to analyze in a likelihood framework (Royle & Dorazio, 2008; Kéry & Schaub, 2011; Schaub & Kéry, 2012). This frees ecologists to focus on developing interesting, relevant models for their systems rather than writing complex likelihood functions (Kéry, 2010; Kéry & Schaub, 2011; Schaub & Kéry, 2012). The consistent treatment of fixed effects, random effects, and missing data is another advantage of the Bayesian paradigm (Link & Barker, 2010; Heisey, 2012). Calculation of derived parameters and out-of-sample predictions, and propagating error associated with these quantities, is simple and does not rely upon asymptotic approximations (Kéry, 2010; Link & Barker, 2010); such derived parameters and predictions are commonly of interest in population models. Updating prior

information with data to produce posterior distributions, a centerpiece of the Bayesian paradigm, is consistent with the way most conservation science progresses (Clark, 2007). Further consistency is gained by the intuitive interpretation of posterior distributions as simple probability statements, which is often how resource managers and the public erroneously interpret frequentist confidence intervals. For these benefits, the cost is the specification of priors (Royle & Dorazio, 2008) and computing time, the latter of which can be substantial for some hierarchical models.

Hierarchical models and their analysis by Bayesian methods are increasingly common in ecology, but we have likely only seen the tip of the iceberg with regard to the utility of these models for the ecologist. Hierarchical models are an area of intense statistical research, and many applications relevant for the ecologist have yet to be realized (Cam, 2012; Heisey, 2012). For many ecologists, training in Bayesian analysis consists of a workshop or self-teaching with one (or more) of the several excellent texts on the subject (e.g., McCarthy, 2007; Royle & Dorazio, 2008; King *et al.*, 2009; Kéry, 2010; Link & Barker, 2010; Kéry & Schaub, 2011). Treatment of Bayesian analysis as standard methodology in biometry and statistical ecology courses is in its infancy, and we reinforce the call of Cam (2012) for advanced courses in statistical modeling for wildlife biologists. As Bayesian methods are incorporated into mainstream statistical training for ecologists, we expect even greater growth in the use and development of hierarchical models for ecological applications.

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